Locally rare species influence grassland ecosystem multifunctionality

Santiago Soliveres[1], Peter Manning[1,2], Daniel Prati[1], Martin M. Gossner[3,4], Fabian Alt[5], Hartmut Arndt[6], Vanessa Baumgartner[7], Julia Binkenstein[8], Klaus Birkhofer[9], Stefan Blaser[1], Nico Blüthgen[10], Steffen Boch[1], Stefan Böhm[11], Carmen Börschig[12], Francois Buscot[13,14], Tim Diekötter[15], Johannes Heinze[16], Norbert Hölzel[17], Kirsten Jung[11], Valentin H. Klaus[17], Alexandra-Maria Klein[18], Till Kleinebecker[17], Sandra Klemmer[13], Jochen Krauss[19], Markus Lange[3, 20], E. Kathryn Morris[21,22], Jörg Müller[16], Yvonne Oelmann[5], Jörg Overmann[7], Esther Pašalić[3], Swen C. Renner[11,23], Matthias C. Rillig[22,24], H. Martin Schaefer[25], Michael Schloter[26], Barbara Schmitt[1], Ingo Schöning[20], Marion Schrumpf[20], Johannes Sikorski[7], Stephanie A. Socher[27], Emily F. Solly[20], Ilja Sonnemann[22], Elisabeth Sorkau[5], Juliane Steckel[19], Ingolf Steffen-Dewenter[19], Barbara Stempfhuber[26], Marco Tschapka[11], Manfred Türke[14,28], Paul Venter[6], Christiane N. Weiner[19], Wolfgang W. Weisser[3,4], Michael Werner[19], Catrin Westphal[29], Wolfgang Wilcke[30], Volkmar Wolters[31], Tesfaye Wubet[13], Susanne Wurst[32], Markus Fischer[1,2], Eric Allan[1]

[1]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland. [2]Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre BIK-F, Senckenberganlage 25, 60325 Frankfurt, Germany. [3]Institute of Ecology, Friedrich-Schiller-University Jena, Dornburger Straße 159, D-07743 Jena, Germany. [4]Technische Universität München, Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. [5]Geocology, University of Tuebingen, Ruemelinstr. 19-23, 72070 Tuebingen, Germany.[6]Universität zu Köln, Biozentrum Köln, Zülpicher Str. 47b, 50674 Köln.[7]Leibniz Institute DSMZ-German Collection of Microorganisms and Cell

Cultures, Inhoffenstr. 7B, 38124 Braunschweig, Germany.[8]Institute for Biology 1, Albert Ludwigs-University Freiburg, Hauptstr. 1, 79104, Freiburg, Germany.[9]Department of Biology, Lund University.[10]Ecological Networks, Biology, Technische Universität Darmstadt, Schnittspahnstr. 3, 64287 Darmstadt. [11]Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany. [12]Agroecology, Department of Crop Sciences, Georg-August University of Göttingen, Grisebachstr. 6, D-37077, Göttingen, Germany. [13]UFZ-Helmholtz Centre for Environmental Research, Department of Soil Ecology, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany. [14]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103 Leipzig, Germany. [15]Department of Landscape Ecology, Kiel University. [16]Biodiversity Research / Systematic Botany, University of Potsdam, Maulbeerallee 1, D-14469 Potsdam, Germany. [17]Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany. [18]Nature Conservation and Landscape Ecology, University of Freiburg, Germany. [19]Department of Animal Ecology and Tropical Biology, Biocentre, University of Würzburg, Am Hubland, D-97074 Würzburg, Germany. [26]Max-Planck Institute for Biogeochemistry, Hans-Knoell-Str. 10, 07745 Jena, Germany. [21]Xavier University, Department of Biology, 3800 Victory Parkway, Cincinnati, OH 45207. [22]Plant Ecology, Institut für Biologie, Freie Universität Berlin, Altensteinstr. 6, D-14195 Berlin. [23]Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Road, Front Royal, VA 22630 US. [24]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany. [25]Department of Ecology and Evolutionary Biology, Faculty of Biology, University of Freiburg, Hauptstraße 1, 79104 Freiburg i. Br., Germany. [26]Research Unit for Environmental Genomics; Helmholtz Zentrum München, Ingolstädter Landstr. 1, 85758 Oberschleissheim, Germany. [27]Department of Ecology and Evolution, Universität Salzburg, Kapitelgasse 4-65020 Salzburg, Austria. [28]Institute for Biology, Leipzig University, Johannisallee 21, D-04103 Leipzig, Germany. [29]Agroecology, Department of Crop Sciences,

Georg-August University of Göttingen, Grisebachstr. 6, D-37077, Göttingen, Germany.
[30]Institute of Geography and Geoecology, Karlsruhe Institute of Technology (KIT), Reinhard-Baumeister-Platz 1, 76131 Karlsruhe, Germany. [31]Department of Animal Ecology, Justus-Liebig-University Giessen. [32]Institut für Biologie Funktionelle Biodiversität, Freie Universität Berlin. Königin-Luise-Str. 1-3. D-14195 Berlin.

***corresponding author**: santiago.soliveres@ips.unibe.ch

Abstract

Species diversity promotes the delivery of multiple ecosystem functions (multifunctionality). However, the relative functional importance of rare and common species in driving the biodiversity-multifunctionality relationship remains unknown. We studied the relationship between the diversity of rare and common species (according to their local abundances, and across nine different trophic groups) and multifunctionality indices derived from 14 ecosystem functions on 150 grasslands across a land-use intensity gradient. The diversity of above- and belowground rare species had opposite effects, with rare aboveground species being associated with high levels of multifunctionality, probably because their effects on different functions did not trade-off against each other. Conversely, common species were only related to average, not high, levels of multifunctionality, and their functional effects declined with land-use intensity. Apart from the community-level effects of diversity, we found significant positive associations between the abundance of individual species and multifunctionality in 6% of the species tested. Species-specific functional effects were best predicted by their response to land-use intensity: species that declined in abundance with land-use intensification were those associated to higher levels of multifunctionality. Our results highlight the importance of rare species for ecosystem multifunctionality and help guiding future conservation priorities.

Keywords: biodiversity, common species, ecosystem function, ecosystem services, grasslands, identity hypothesis, land use, multi-trophic

1. Introduction

Many studies have demonstrated that high species diversity enhances ecosystem functioning both in experimental and natural assemblages (1-4; reviewed in [5] this issue). However, it has been argued elsewhere that it is not the total number of species *per se*, but the functional properties of the most locally abundant ones (hereafter common species) that drive ecosystem functioning (mass-ratio hypothesis; [6]). Other work has shown that each common species can only provide a limited number of functions [1, 7-8]. Extending the mass-ratio hypothesis to the simultaneous provision of multiple ecosystem functions at high levels (multifunctionality), we might therefore predict that several common species would be needed to maintain multifunctionality and that the diversity of common species, rather than overall diversity, would be its main biotic driver. In contrast to this argument, less locally abundant (hereafter rare) species have been shown to play a crucial role in affecting several ecosystem functions [9-11]. Rare species comprise the vast majority of the species in any natural community and are more sensitive to anthropogenic disturbances [12, 13]. Thus quantifying the functional consequences of their loss is of particular importance to predict the provision of ecosystem services in the future. The functional importance of common vs. rare species could depend on the ecosystem functions under scrutiny. Studies focused on productivity and pollination have found common species to be the main driver (e.g., [9, 14-17]) while those focusing on functions associated with some regulating (e.g., invasion resistance) or recreational (e.g., bird watching) services highlight the importance of rare species [18-20]. Due to their contrasting effects depending on the function considered, studies measuring multifunctionality are required to comprehensively assess the relative functional importance of rare and common species [8, 11].

Studies across large temporal or spatial scales have shown that the relationship between diversity and ecosystem functioning may change with abiotic conditions or land-use intensification [21-25], the level of multifunctionality desired [8, 26] or the type of organism

being considered [23]. Land-use intensification promotes shifts in the functional composition of multiple taxa (e.g., 27), potentially dampening the generally positive relationship between diversity and ecosystem multifunctionality (25). The effects of biodiversity might also depend on the level of multifunctionality considered [26, 28]. High levels of many functions can be difficult to achieve if there are strong trade-offs between functions or between diversity effects on these functions. Finally, different components of biodiversity may differ in their functional effects. Above- and belowground organisms differ in their sensitivity to climate or anthropogenic disturbances, with rare aboveground species being the most sensitive (e.g., [13, 29]), and can also have different effects on ecosystem multifunctionality, with stronger effects found for aboveground organisms [23, 30]. The context-dependencies of the biodiversity-functioning relationship are poorly understood, particularly in terms of how they might modify effects of rare and common species. Existing comparisons of the functional role of rare vs. common species have seldom been extended beyond single taxa, individual ecosystem functions or a particular study site (but see [11]). In order to understand the response of natural and semi-natural ecosystems to ongoing global change, we therefore need to examine the relationships between different components of diversity (above- vs. belowground, common vs. rare) and ecosystem multifunctionality across environmental gradients [23] (see also [31]; this issue).

It has also been hypothesized that the presence of certain species can be of particular importance for ecosystem functioning, regardless of their abundance or whether they are above- or belowground organisms (identity hypothesis; [32, 33]). This hypothesis has received empirical support from studies focusing on individual functions such as litter decomposition, parasitism or predation [34-36]. However, studies have not yet tested whether there are species that can drive overall ecosystem multifunctionality, which would require lack of trade-offs in their effects on different functions. If there are influential species, it is important to understand the characteristics that they possess and how they respond to land-use

intensification. If such species decline in abundance as land use intensifies then, in addition to effects of biodiversity loss, compositional change driven by land use may have large effects on ecosystem multifunctionality.

Here, we assess the functional role of the diversity of rare and common species (based on their local abundance), both above- and belowground, on several multifunctionality indices derived from 14 ecosystem functions, related to the delivery of supporting, provisioning, regulating and cultural services (*sensu* [37]). Our hypotheses are: i) the diversity of common species is a more important driver of ecosystem multifunctionality than the diversity of rare species, ii) the positive effect of diversity on multifunctionality will decline with land-use intensity due to the associated changes in functional composition, iii) the diversity of aboveground organisms is the strongest biotic predictor for ecosystem multifunctionality [23], iv) there are particular species, across multiple trophic levels, that can promote high multifunctionality and land-use intensification changes the abundance of these species.

2. Material and methods

(a) Study sites

We sampled 150 grassland plots (50 m × 50 m) equally distributed over three regions across Germany: the UNESCO Biosphere Reserves Schwäbische Alb (located in the Southwest) and Schorfheide-Chorin (in the Northeast), and the area in and around the National Park Hainich-Dün (in central Germany; [38]). The 50 grassland plots per region were selected to span a gradient of the full range of land-use practices and intensities found in Central European grasslands. Information about land-use intensity was obtained directly from the land owners via questionnaires [38]. We used this information to calculate a compound measure of land-use intensity (LUI) which summarizes the three major components of land-use in these grasslands -intensity of fertilization, mowing and grazing- with the following formula: LUI = sqrt((F_i/F_R) + (M_i/M_R) + (G_i/G_R)), where F_i, M_i and R_i are the amount of fertilizer applied,

frequency of mowing cuts, and standardized units of livestock density within each sampling site per year, respectively. All three components were standardized by the average across the 50 grassland plots within each region (F_R, M_R and G_R; see [39] for full methodological details). We averaged LUI across 2006-2010, the period when most diversity and functioning data was collected.

(b) Analyses at the community level

(i) Diversity measures

At each site, we measured the abundance and richness of nine trophic groups using standard methodology (see Table S1 for details). Overall, our sampling included ~4300 taxa (the taxonomic unit varied between groups [Table S1] but we refer to all as *species*, for simplicity). The groups were: autotrophs (plants and bryophytes), belowground herbivores (insect larvae), belowground predators (insect larvae), detritivores (insects and millipedes), soil microbial decomposers (bacteria), aboveground herbivores (insects), aboveground predators (insects, spiders and centipedes), arbuscular mycorrhizal fungi and belowground bacterivores (bacterivorous protists). Omnivorous arthropods were not considered in our analyses as there were too few of them.

Using data for each of these nine trophic groups we calculated multidiversity, i.e., a measure of overall diversity at the community level obtained by averaging standardized diversity measures across trophic groups [13]. To calculate multidiversity we first classified the species into two groups according to their abundance (which was measured differently for the various groups [Table S1]): common (the top 10% species in terms of total abundance) and rare species (the bottom 90% of species). Abundance is widely accepted as a measure of rarity (e.g., [40]); therefore, we chose abundance across all study sites to be the most representative measure of the overall rarity of our target species. The top 10% species (*common* species hereafter) accounted for 80% of the total abundance sampled, whereas the

bottom 90% of species (*rare* species hereafter) made on average 20% of the total abundance (ranging from 6% in bacteria to 30% in belowground herbivores; Fig. S1). A second step in the calculation of our multidiversity metric was to standardize all variables to a common scale (between 0 and 1) by subtracting the minimum value and dividing by the maximum value found across the 150 sites to avoid the influence of different ranges in diversity characterizing each group. Third, we classified the trophic groups into above- and belowground organisms (plants were considered aboveground organisms). Finally, we averaged their standardized values to obtain four measures of multidiversity: above- and belowground common species multidiversity, and above- and belowground rare species multidiversity.

(ii) Ecosystem function measures

At each site, we measured 14 different ecosystem functions. These were: aboveground and belowground plant biomass, root decomposition rates, potential nitrification, soil phosphorus retention, arbuscular mycorrhizal fungal root colonization, stability of soil aggregates, soil organic carbon, forage quality, resistance to aboveground plant pathogens, aboveground pest control, pollinator abundance, bird diversity and flower cover (see [25] and Table S2 for detailed methodology). These ecosystem functions are related to nutrient cycling, food provision, sustainable soil use, pest resistance, or cultural and recreational services. We calculated three ecosystem multifunctionality metrics using these 14 functions and following the multiple threshold approach of Byrnes *et al*. [26], which sum up the number of measured functions that exceeds a given threshold. These thresholds are defined as a given percentage of the maximum level found for each function, and we used three thresholds (50%, 75% and 90%) to represent a wide spectrum. In order to reduce the influence of outliers the maximum was defined as an average of the top five values for each function across our study sites.

(iii) Statistical analyses

We used multi-model inference based on information theory [41] to analyze the response of ecosystem multifunctionality to the multidiversity of above- and belowground common and rare species. We performed a different analysis for each of the three multifunctionality metrics. Large-scale studies such as ours allow quantifying the relative importance of diversity regarding other drivers of ecosystem functioning, and also to evaluate changes in diversity-functioning relationships across contrasting environmental conditions. However, it is difficult from observational studies to infer causality as diversity-functioning relationships could be confounded by environmental factors affecting both diversity and ecosystem functioning. To avoid the latter, we controlled for factors that could affect both multidiversity and ecosystem functioning in our analyses; these were study region, environmental variables (pH, soil depth and topography [an index based upon the position and steepness of each site, which is related to the accumulation of soil material and water availability; [42, 43]) and LUI. We removed elevation from the set of environmental predictors because it was highly correlated with soil depth (Spearman´s rank correlation ρ = -0.91). We also accounted for potential context-dependencies in the diversity-multifunctionality relationship by including the interactions between LUI, region, and the four multidiversity predictors.

To analyze the relative importance of environmental conditions, the multidiversity of above- and belowground common and rare species, and the interactions between them, as drivers of ecosystem multifunctionality, we built a set of competing models including either: environmental variables only, environmental + diversity variables, or environmental + diversity variables and the interactions between diversity and region and/or land-use intensity; see Table S3 for the full list of models). From these competing models we selected those that best fit our data according to the Akaike Information Criterion (AICc, corrected for small sample sizes). Thus, those models differing less than 2 AICc units from the most parsimonious model (ΔAICc < 2) were included in the set of best-fitting models. We also

calculated the importance of our different predictors as the sum of the AICc weights (a comparison with each model´s AICc with the minimum AICc) of the models in which each predictor appears. To allow comparisons between main effects and interaction terms, we divided the importance of each predictor by the number of models in which it was included (16 for the diversity predictors [maximum importance 1/16], and eight for their interactions with region and LUI [maximum importance 1/8]; see [44] for a related approach).

As a sensitivity analysis, we repeated our multi-model selection but used the multidiversity of the bottom 50% species, instead of the bottom 90%, as an alternative measure of rarity. These bottom 50% species made up on average 3% of the total abundance (ranging from 0.04% in bacteria to 6% in belowground herbivores; Fig. S1; see Table S4 for detailed results). We also repeated our analyses using the abundance, instead of the species richness, of above- and belowground common and rare species (Table S5). Results of sensitivity analysis were broadly similar to the main ones and therefore are not further discussed.

(c) Analyses at the species level

(i) Selection of species

We selected a subset of individual species that occurred in all three study areas, and in at least 10 of the 150 sites to obtain reliable parameter estimates (see *Estimation of the functional role of each species* below). Some of the trophic groups measured (detritivores, and belowground herbivores and predators) were not included in these species-level analyses as they contained too few species fulfilling our selection criteria. Of those that did, soil microbial decomposers and bacterivorous protists were overrepresented. Thus, in order to obtain a balanced sampling size for each trophic group, we only selected the most and least abundant 25 species within each trophic group that met the criteria. These species roughly corresponded to those classified as common and rare in the community-level analyses (Table S6). Thereby, we

obtained a balanced sample size of 50 species per trophic group (~50% of them common, ~50% rare), with the exception of aboveground predators, for which only 20 species met our criteria (270 species considered overall).

(ii) Estimation of the multifunctional role of each species

To estimate the multifunctional role of each species, we used the null model approach of Gotelli *et al*. [45] as implemented by the software *Impact* [46]. This analysis allowed us to identify the presence of influential species, and whether or not the degree of functional influence was related to the average species´ abundance, to their functional traits or to their response to land-use intensity. The latter allowed us to test for the effects of compositional changes, across trophic levels, driven by land-use intensification on multifunctionality. This analysis further allows us to identify whether there are functional trade-offs within each trophic level; i.e. whether some species within a group are significantly associated with multifunctionality. The null-model approach used performs linear regressions between the abundance of each species and a given function, and then compares the observed slope with 1000 random permutations of the values of the functional variable. From the randomizations, a standardized effect size (SES) for each species is calculated as: $SES = (S_{obs} - S_{sim})/SDev$; where S_{obs} and S_{sim} are the observed and the average of the 1000 simulated regression slopes, respectively, and SDev is the standardized deviation of the slopes obtained from these 1000 randomizations. SES values higher than 2 or lower than -2 show significant relationships between the abundance of a given species and the function used as a response. We used our three multifunctionality measures as a response and thus obtained three functional effect sizes for each of our target species (270 target species × 3 multifunctionality scenarios = 810 comparisons). Due to the increased type II error derived from multiple testing, 40 of these 810 comparisons would be expected to be significant only by chance; we found two times more

288 significant results (Table S7), implying that our results are unlikely caused by multiple testing
289 only.
290 By randomizing the functional variable instead of the species abundances, the null
291 model approach takes partially into account the structure of the biotic community (including
292 species interactions and non-independent effects; see full discussion in [45]). However, this
293 method is purely correlative and prone to confounding factors which could be driving both the
294 function and the abundance of the target species. To control for the latter we used the
295 residuals of both the abundance of each species and the multifunctionality metrics after
296 filtering for the same environmental variables used in the multi-model selection (region, LUI,
297 soil pH and depth, elevation, and topography). Despite its limitations, this is to our knowledge
298 the best method available to estimate the functional effects of many species (which would be
299 logistically prohibitive to address experimentally).
300
301 *(iii) Statistical analyses*
302 We performed two complementary analyses at the species-level. First, to assess the functional
303 importance of above- and belowground groups, and of rare and common species, we
304 compared their number of significant positive and negative standardized effect sizes (SES) in
305 each of the four categories of species, using Fisher´s exact tests (better suited for low sample
306 sizes than χ^2 analyses). This allowed us to assess if there are influential species related to
307 multifunctionality, and if these are either common or rare, or mainly represented by above- or
308 belowground organisms. The second analysis aimed to understand further which features
309 makes a species influential for multifunctionality. To do this we performed multiple
310 regressions with the SES of the functional effect of each species as a response variable, and
311 the "response to land-use intensity" as a predictor. To correct for other species characteristics
312 that might affect their multifunctional importance, we also included their average abundance
313 (across all sites in which each species occurred) and functional traits (plant height and specific

leaf area for plants, and body size for herbivores and predators; obtained from available databases [47, 48]). "Response to land-use intensity" was the standardized coefficient of a linear regression between each species´ abundance and LUI. The number of sites in which each species occurred (which was correlated also with the range in abundance values; ρ = 0.45) was introduced as covariate in our analyses as it could affect slope estimates in the null-model approach used. The traits selected are related to species responses to LUI [25, 49, 50] and also play an important role for ecosystem functioning [25, 51]. Data on functional traits was not available for microbial decomposers, bacterivorous protists and symbionts. Context-dependencies in the species-level analysis were accounted for by including the interaction between region, trophic group, and abundance or response to LUI as extra predictors. The interactions with region were not significant in any case and therefore they are not considered further. All analyses were performed using R version 3.0.2 [52].

3. Results

(a) Community level

Between 10% and 18% of the variation in multifunctionality was explained by study region, environmental variables, land-use intensity (LUI) and our multidiversity metrics (Fig. 1). All the best models (those with $\Delta AIC < 2$) included at least one of the four multidiversity metrics, with models only including environment and LUI performing less well (ΔAIC between 2.6 and 7.1; Table S3). The effects of multidiversity on multifunctionality differed depending on the metrics considered. Aboveground multidiversity of common species was not significantly related to any of the multifunctionality measures, whereas the multidiversity of common species belowground was positively related to multifunctionality at the 50% threshold, but not to the other multifunctionality measures (Table S3). The multidiversity of rare species both above- and belowground was significantly, but oppositely (positive for above- and negative

for belowground), related to multifunctionality at the highest thresholds (75% and 90%; Figs. 1 and 2).

The relationships found between multidiversity (both above- and belowground) and multifunctionality at the highest thresholds did not depend on LUI or study region (Fig. 1). The best models for both the 75% and 90% thresholds did not include interactions between region and/or LUI and multidiversity (Table S3). The best models for the 50% multifunctionality threshold, however, included interactions between region, and/or LUI, and one or more multidiversity metrics (Fig. 1; Table S3), thus demonstrating that multidiversity-multifunctionality relationships were context-dependent for the low threshold measure. Indeed, for multifunctionality at the 50% threshold the interactions were as important as the main effects (Fig. 1), and not including them increased the AICc by more than 3 units in all cases, suggesting a strong decline in model performance (Table S3). Interactions with region or LUI affected the associations between belowground, but not aboveground, multidiversity and multifunctionality. The association between the multidiversity of belowground common species and multifunctionality was positive in the southwest, neutral in the central region and negative in the northeast (see interaction coefficients in Fig. S2). LUI also influenced the effect of belowground multidiversity, with associations between the multidiversity of both rare and common species and multifunctionality becoming more positive with decreasing LUI (Fig. S2). Regardless of the interactions with region and LUI, we found a higher importance of aboveground multidiversity for the 75% and 90% thresholds, which shifted towards a higher importance of belowground multidiversity components at the 50% thresholds (Fig. 1; Table S3).

(b) Species level

Apart from the community-level effects of multidiversity, we found significant positive associations between the abundance of individual species and multifunctionality in 6% of the

365 species tested, whereas we found negative relationships for 4% of the species (Table S7).
366 Aboveground rare species had significantly more positive, and fewer negative, relationships
367 with multifunctionality than the aboveground common species did (Fig. 3), a trend not found
368 in belowground organisms. The ratio between positive and negative relationships differed
369 substantially depending on the trophic group studied. Microbial decomposers had more
370 positive than negative relationships with multifunctionality (11% vs. 1%), with the opposite
371 pattern observed in symbionts (4% vs. 10%, Table S7). The remaining trophic groups showed
372 slightly more positive than negative relationships.
373 Including the abundance, functional traits and response to LUI of the individual
374 species allowed us to predict 13-16% of the variance in the strength of species –
375 multifunctionality associations. The multiple regressions performed revealed that response to
376 LUI was the strongest predictor of the associations between individual species abundance and
377 multifunctionality. Species that increased in abundance in response to LUI were negatively
378 correlated with multifunctionality at the 75% and 90% thresholds (Fig. 4; Table S8).
379
380 ## 4. Discussion
381
382 ### (a) Effects of the multidiversity of rare and common species on multifunctionality
383
384 The important role that rare species play in maintaining individual ecosystem functions and,
385 to some extent, multifunctionality has been highlighted previously [8, 11, 18-20]. Here, we
386 extend those results to multitrophic assemblages in realistic landscapes, and show that: i) the
387 relative importance of rare species increases when multifunctionality is defined using higher
388 thresholds for the functions and ii) that this relationship remains relatively consistent across
389 study regions and land-use intensities (Fig. 2). Our results show that the ability of ecosystems
390 to maintain a large number of functions at average levels (50% threshold) is mainly driven by

391 the diversity of common species and, intuitively, by the prevailing environmental conditions
392 (as shown by the significant interactions found in our models). However, the delivery of a
393 smaller number of functions, but at very high levels (75% and 90% thresholds), was mainly
394 related to the multidiversity of rare species. The level of multifunctionality required will
395 depend on stakeholder preferences, but the performance of many functions at their highest
396 potential (high multifunctionality values at high thresholds) can be generally interpreted as a
397 more desirable state of natural ecosystems. Overall, our study shows that the diversity of rare
398 species is consistently and positively related to multifunctionality at the highest levels, thus
399 implying the existence of "win-win" scenarios between biodiversity conservation and
400 ecosystem service provision.

401 A high diversity of rare species might be more beneficial for multifunctionality than a
402 high diversity of common species if rare species are less likely to negatively affect ecosystem
403 functions. We found that functional trade-offs between species, where some species have
404 positive effects on multifunctionality and others negative effects, were less common amongst
405 rare than common species (Fig. 3). This could explain the stronger positive effect of rare
406 species diversity on multifunctionality. Our correlative study does not allow us to investigate
407 the mechanisms behind the lower incidence of such functional trade-offs in rare species.
408 However, we speculate that if functional effects are driven by the presence of a given species,
409 rather than by its abundance, they are much less likely to be negative. In the case of presence-
410 based functional effects the species is either there, and promotes a given function, or is absent
411 and has no effect. For example, the presence of certain species can promote recreational
412 services such as birdwatching [20], or prevent plant invasions [18, 19]). Such presence-based
413 effects are likely to be the dominant ones amongst rare species. In contrast, functional effects
414 that are proportional to a species' abundance [6] may also be negative. Abundant species can
415 reduce, instead of promote a given function, e.g., species with low specific leaf area can
416 reduce rates of nutrient cycling. Common species are more likely than rare species to have

such abundance-related effects. Therefore, even if the common species are functionally relevant, they may have opposing functional effects (e.g., the positive effects of a common productive plant on forage production might be balanced by negative effects of a common herbivorous insect that feeds upon it). Such strong functional trade-offs between common species could therefore result in a small effect of common species diversity on multifunctionality and a greater importance of rare species diversity in promoting multifunctionality. A complementary explanation for the higher functional importance of rare species is that they tend to be less redundant than common species in the functional traits they possess and, therefore, support communities with more distinct combinations of functional traits [53]. This enhanced functional diversity could also explain the positive functional effect of the multidiversity of rare species, as functional diversity is related to the provision and stability of multiple ecosystem functions [54, 55].

While our study provides unique insights regarding the role of community-level diversity on the provision of multiple functions simultaneously, the use of these aggregate metrics obscures detailed information regarding the relationships between specific taxa and functions. A full description of such functions is outside the scope of this study but could partially explain the relatively low R^2 of our models (< 0.20%; see [56] for a full discussion on the topic). The trade-offs we observed in the functional effects of common species would, obviously, not apply when studying ecosystem functions in isolation. Another reason for the relatively low proportion of explained variance could be the influence of factors operating at large spatial (i.e., surrounding landscape) and temporal scales (i.e., legacy effects of past land-uses), which were not considered in this study [57].

(b) On the functional role of above- vs. belowground multidiversity

Belowground and aboveground biotic components are known to respond differently to anthropogenic disturbances and are likely to differ in their effects on ecosystem functioning (e.g., [13, 30]); however, very few studies have explored their separate functional roles [23]. We found that aboveground multidiversity, particularly of rare species, was often positively related to multifunctionality at the highest levels, whereas belowground multidiversity was negatively associated with it. Aboveground rare species are highly sensitive to anthropogenic disturbances [13, 29] and these findings suggest that they are also amongst the most functionally important species. Our results support the crucial role of the diversity of aboveground organisms, e.g., plants [1-4, 8], but also herbivores [28] or predators [58] in determining ecosystem multifunctionality.

The stronger positive relationship between above- than belowground diversity with multifunctionality concurs with the only previous study including these two groups separately [23]. It may be argued that the higher importance of above- than belowground components is dictated by the selection of ecosystem functions studied; however, this is unlikely as both our study and Jing et al. [23] included a high proportion of soil-related variables. It seems that, when considered alone, belowground diversity explains variation in multifunctionality that could be mainly due to its correlation with aboveground diversity [23, 58], but further studies are required to test whether the pattern we observed holds across a wide variety of ecosystems and environments. Importantly, our snap-shot sampling design may have reduced our capacity to compare the effects of both above- and belowground multidiversity, as belowground organisms are less sensitive to anthropogenic disturbances [13] and thus they could increase the stability in ecosystem functioning by increasing response diversity [59].

The negative relationship between belowground diversity and ecosystem multifunctionality, however, is surprising and contrasts with previous research (e.g., [23, 60,

61]). Soil biota effects are often driven more by functional composition than by species richness *per se* (see [60] for a review). Hence, the negative relationship between belowground multidiversity and ecosystem functioning could reflect compositional changes rather than diversity effects [23, 24]. Another potential explanation for these results is that the functional effects of belowground diversity are context-dependent and change with climate or soil (regional differences in our study sites [62]), or with land-use intensification (Fig. S2; see also [23]). The latter could obscure the overall effect of belowground multidiversity on ecosystem functioning, when it is investigated across wide environmental gradients. In this regard, we found strong context-dependency for low (50%) levels of multifunctionality, as the relationship between belowground multidiversity and multifunctionality changed both with study region and land-use intensity (Fig. S2). Regardless of the underlying mechanisms, the contrasting relationships between above- and belowground biotic components and multifunctionality highlight the necessity to consider both in order to better understand the functional consequences of biodiversity loss in realistic landscapes.

(c) Individual species´ effects on multifunctionality

Substantial research effort has been devoted to explain the functional role of individual species in natural ecosystems. Previous research suggests that the most abundant species [6], or a few key species with particular functional traits [32], will have the strongest effect on ecosystem functioning. These two hypotheses have received substantial empirical support across a large variety of systems and individual functions [6, 14, 15, 17, 33-36], but have rarely been tested for multiple functions simultaneously, or across multiple trophic groups. In addition to the effects of the diversity of the entire community, for 10% of the species tested, we found a significant relationship between their abundances and multifunctionality. This suggests that, despite potentially contrasting functional effects (positive, negative or neutral,

depending on the function), some species, even individually, influence the overall ability of ecosystems to simultaneously provide multiple functions. This result supports the identity hypothesis [32, 33], extending it to multiple functions and trophic levels. An example of one of these particularly influential species is *Hieracium pilosella*, plant native to central Europe and locally rare in our study sites. This species was positively associated with multifunctionality according to our method and has previously been shown to increase soil organic C, litter decomposition and microbial biomass in comparison to other grassland species [63], to attract a variety of pollinators [64] and to have a relatively high resistance to pathogenic fungal infections [65]. We found a similar number of influential species for both common and rare species, and for both above- and belowground organisms; indicating that individual species within these biotic components are equally important for multifunctionality. Understanding the attributes of these particularly influential species, and their effects on multifunctionality should be a research priority if we are to predict the consequences of biodiversity loss and compositional changes for ecosystem service provision.

The direction of the relationship between the abundance of individual species and multifunctionality was best predicted by their response to land-use intensification, even after accounting for the range in abundance across the plots and important functional traits. Previous studies have shown that land-use intensification shifts plant functional composition and leads to an increase in the abundance of productive species, which enhance some provisioning services but compromise regulating and cultural services such as carbon storage or aesthetic value, therefore reducing overall multifunctionality [25]. Similarly, changes in the ratio between soil fungi and bacteria with land-use intensification may speed-up nutrient recycling but reduce ecosystem recovery after disturbances [24]. We show here that, alongside reducing their diversity, land-use intensification may substantially influence the effect of multiple trophic levels, via compositional changes, on ecosystem functioning. Our results, therefore, suggest that the negative effect of LUI on multifunctionality at high

thresholds could be, at least partly, caused indirectly by the negative response of particularly influential species to land-use intensification. Such compositional changes might be particularly relevant for belowground communities, whose relationships with multifunctionality (50% threshold) became negative under increasing land-use intensity (Fig. S2).

(d) Conclusion

Substantial research effort has raised awareness of the functional consequences of losing biodiversity. However, we are still far from fully understanding which species or biodiversity attributes conservation efforts should focus on if ecosystem services are to be conserved. Our results suggest that locally rare aboveground species are the most important diversity component to preserve high levels of ecosystem multifunctionality in managed grasslands, perhaps due to their lower proportion of negative functional effects. Our multitrophic approach also supports the identity hypothesis, and extends it to multiple trophic groups and functions by showing, for the first time, that ~10% of the species tested can be particularly associated to overall ecosystem functioning. We also found that the effect of an individual species on multifunctionality is related to its response to land-use intensity, which will help to anticipate the functional consequences of compositional changes across multiple trophic groups caused by land-use intensification.

Authors' contributions

SS and EA conceived the study, all the authors but SS and EA gathered the data, MG compiled the trait data, SS and EA did the analyses, SS wrote the first draft and all co-authors significantly contributed to improve it.

Competing interests

We declare we have no competing interests.

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Supporting Information

Additional Supporting Information may be downloaded via the online version of this article at the journal website (http://rstb.royalsocietypublishing.org).

Table S1. Details of diversity measurements.

Table S2. Details of ecosystem functioning measurements.

Table S3. Multi-model selection presented in the main text.

Table S4. Multi-model selection of the analyses with the 50% (instead of the 90%) least abundant species as a measure of rare species.

Table S5. Multi-model selection of the analyses with abundance instead of diversity.

Table S6. Summary of the data at the species level (Excel file).

Table S7. Species-specific functional effects organized by trophic group.

Table S8. Multiple regression results (species-level analysis).

Figure S1. Abundance distribution of common and rare species within each trophic group.

Figure S2. Standardized coefficients obtained from model averaging.

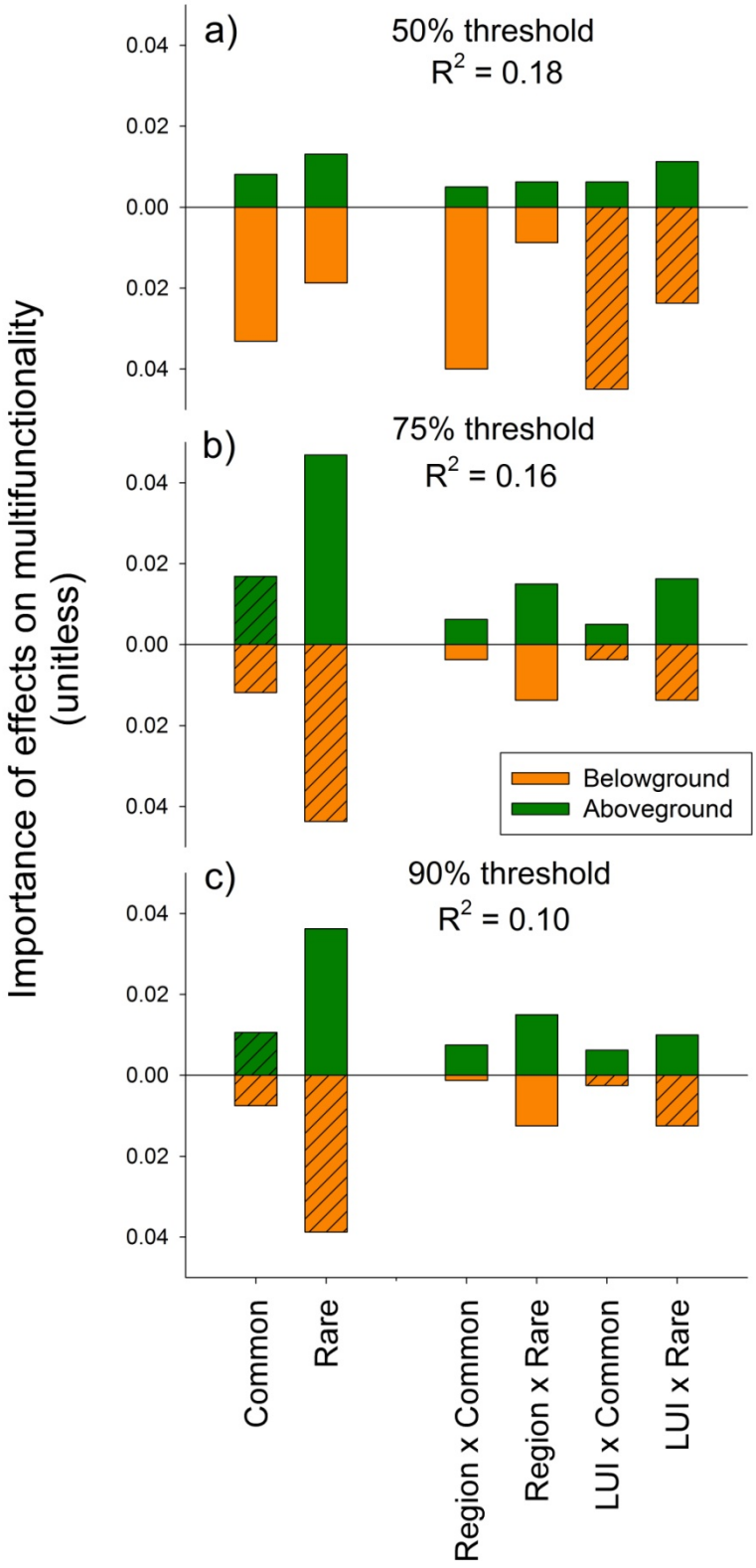
Figure captions.

Figure 1. Importance of the different multifunctionality predictors as assessed by the sum of the AIC weights of the models in which each one was retained, divided by the number of models in which each variable was introduced. Green and brown indicate predictors associated with above and belowground multidiversity, which included the overall diversity of plants, bryophytes, and herbivore, carnivore and decomposer arthropods [aboveground] and soil bacteria, bacterivore protists, arbuscular mycorrhizal fungi and herbivore and carnivore insects [belowground]). Hatched bars indicate negative effects. Common = multidiversity of the top 10% most abundant species (80% of the individuals sampled), rare = multidiversity of the 90% least abundant species (20% of the individuals sampled). Region × indicates the interaction term between study region and a given multidiversity metric. LUI × indicates the interaction term between land-use intensity and a given multidiversity metric. The R^2 of the best model for each multifunctionality metric (first row in Table S3) is provided.

Figure 2. Effect of multidiversity of above- and belowground, common and rare species on the different levels of multifunctionality. Slopes (with confidence intervals) were calculated after controlling for the other predictors in the model, and are shown in blue if selected in the best models (see Table S3; Fig. S2). Note that dots are residuals of both multidiversity and multifunctionality metrics after filtering by study region, LUI, soil pH and depth and the topographic wetness index.

Figure 3. Summary of the relationships between individual species and multifunctionality. The percentage (according to the number of species tested) of significant positive (green) and negative (red) effects are shown. The averaged results across each category (common vs. rare species, aboveground and belowground) are shown. Significant differences ($P < 0.05$)

794 comparing the proportion of positive and negative effects in common and rare species
795 according to Fisher´s exact test are highlighted as "*" ("ns" not significant).
796
797 **Figure 4**. Relationship between the effect of each species (dots) on multifunctionality
798 (standardized effect size) and its response to land-use intensity (LUI). Different colors in dots
799 and lines indicate the relationship found for each trophic group (slopes calculated after
800 filtering by number of sites and average abundance). The black lines indicate the overall
801 relationship (after filtering for the same factors, and trophic group). Response to land-use
802 intensity was measured as the standardized slope of a regression between LUI and the
803 abundance of each species.
804



805

806 **Figure 1**

807

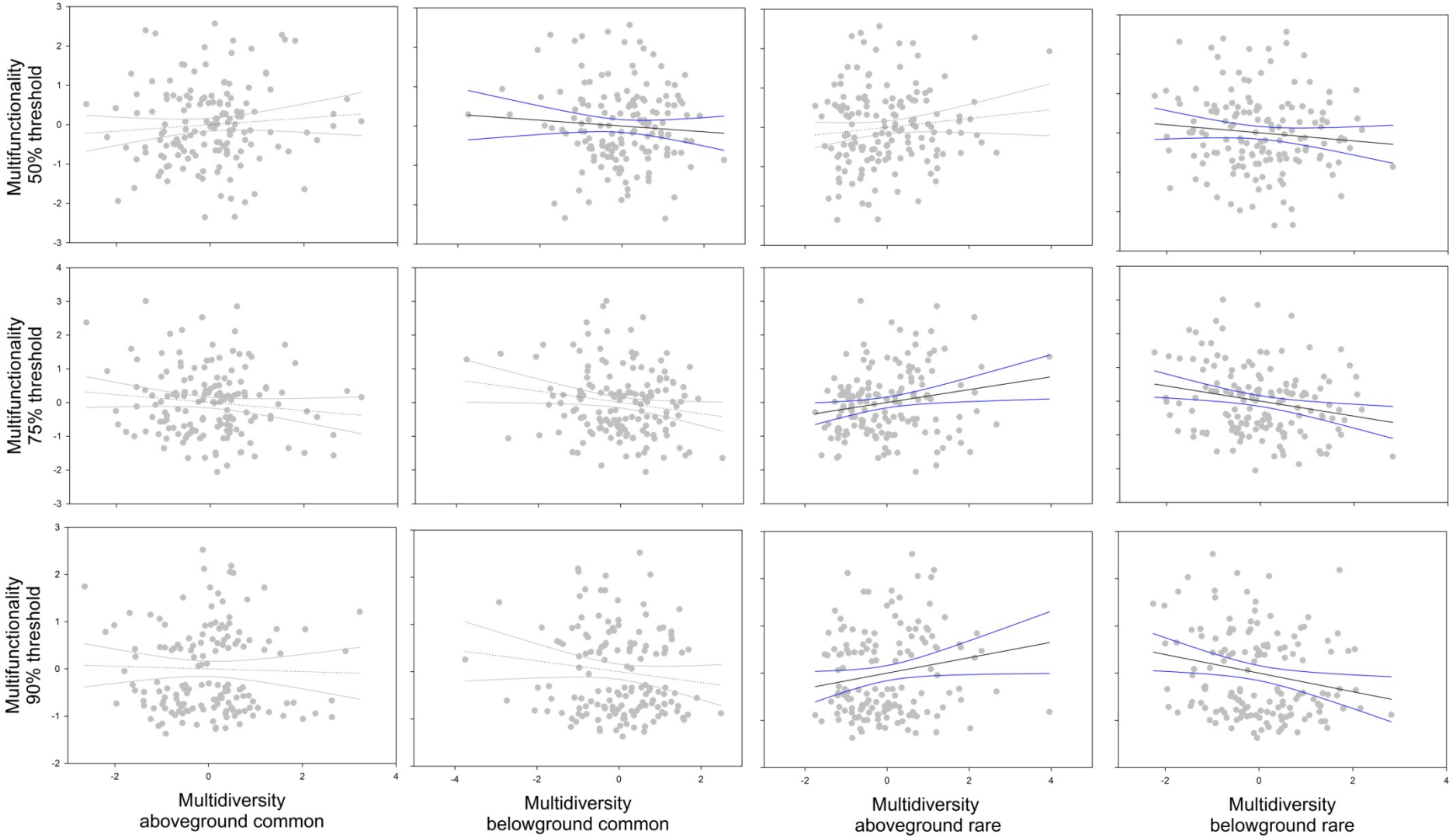

Multifunctionality 50% threshold
Multifunctionality 75% threshold
Multifunctionality 90% threshold
Multidiversity aboveground common
Multidiversity belowground common
Multidiversity aboveground rare
Multidiversity belowground rare

Figure 2

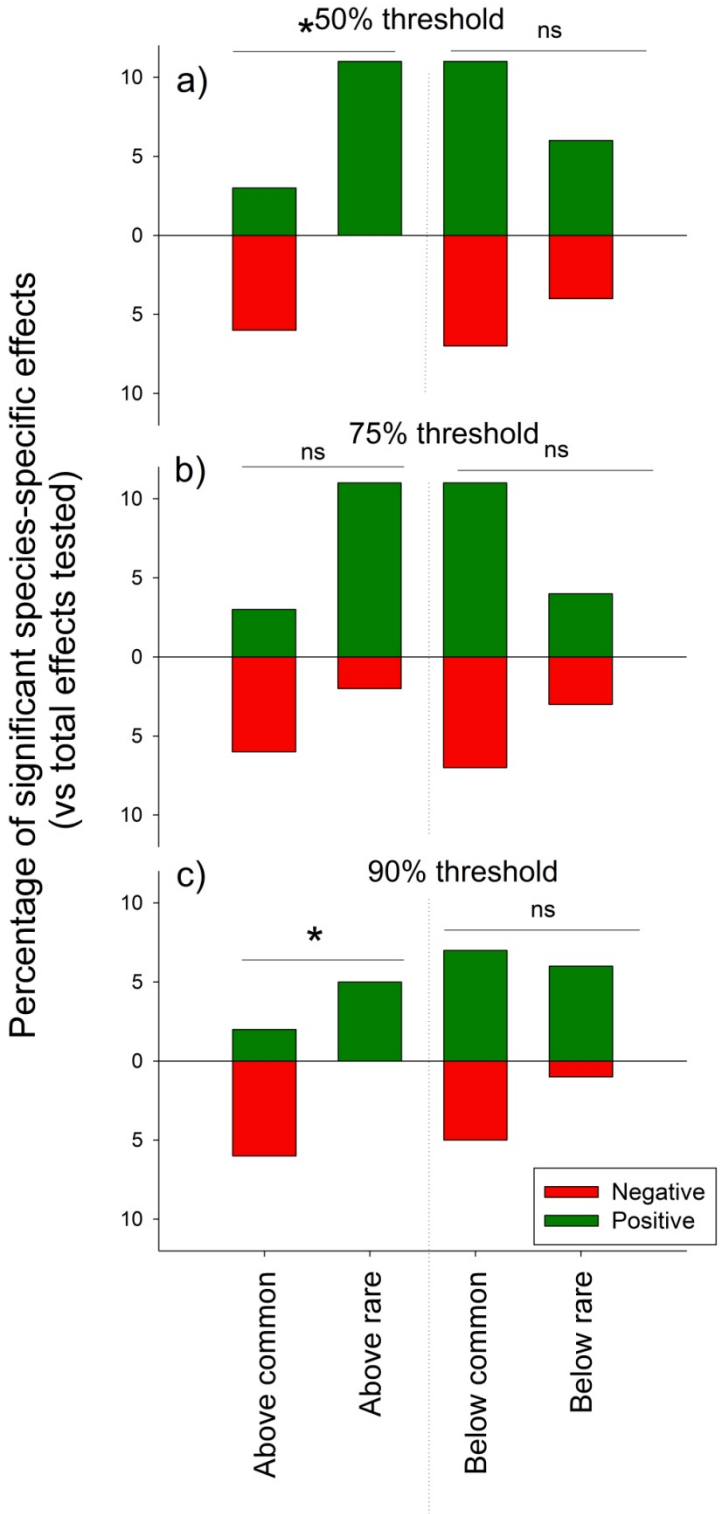
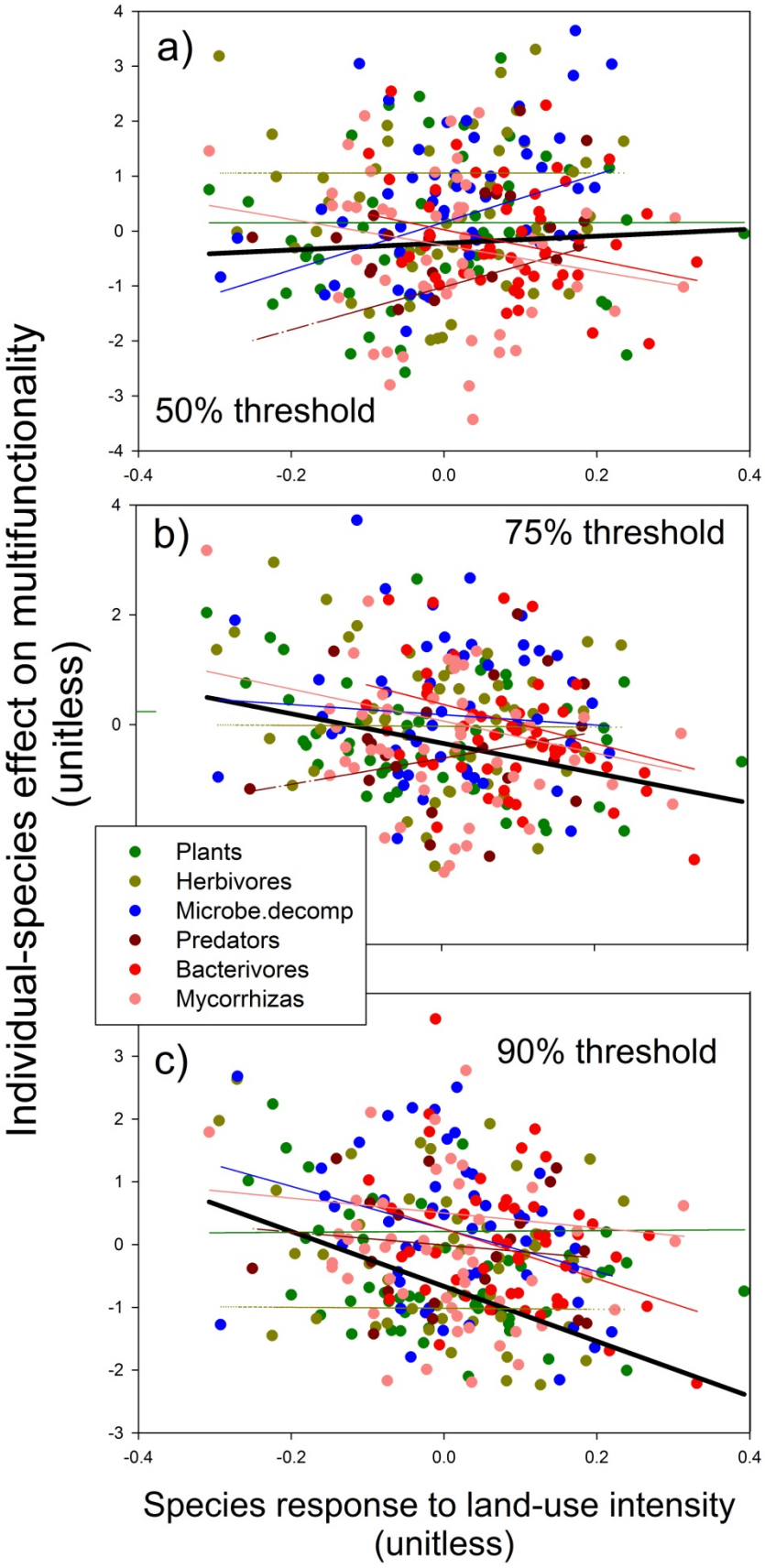

*50% threshold
ns
a)
75% threshold
ns
ns
b)
90% threshold
ns
*
c)
10
5
0
5
10
Percentage of significant species-specific effects
(vs total effects tested)
Negative
Positive
Above common
Above rare
Below common
Below rare

Figure 3



814

815 **Figure 4**